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A New Species of Forest Mouse, Genus *Apomys* (Mammalia: Rodentia: Muridae), from Camiguin Island, Philippines

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Abstract

An inventory of the mammals of Camiguin Island conducted in 1994 and 1995 documented the presence of a previously unknown species of Philippine forest mouse of the endemic Philippine genus *Apomys*, which is here named and described. Based on molecular data, the new species is most closely related to two species (*A. hylocoetes* and *A. insignis*) from Mindanao Island and to an unnamed species from Leyte, Biliran, and Bohol islands. The new species is diagnosed in comparison to its three closest relatives on the basis of slightly browner and less russet fur, slightly greater size overall, a moderately long and broad hind foot with small plantar pads, large tail scales, slightly narrower zygomatic width and mastoid breadth, deep rostrum of moderate length, a long orbit and braincase, narrow palate, large incisive foramina, short distance from the posterior edge of the incisive foramina to the anterior edge of the first upper molar, bony palate that extends well to the posterior of the posterior edge of the last upper molar, bullae that are more strongly oriented toward the cranial midline axis, third upper molar without a conspicuous anterolabial cusp, and a number of more subtle features. It is one of two species of mammals now known to be endemic to Camiguin, the other being *Bullimus gamay* (Rickart et al., 2002). Both are common in rain forest on Camiguin Island at upper elevations. The presence of two endemic mammals on this small (265 km^2) island is remarkable; there are no smaller islands in the Philippines known to support endemic mammal species.

Introduction

The Philippine Islands are notable for their large number of unique species of mammals; of 172 species known in 1998, 111 (64%) occurred nowhere else in the world, one of the greatest concentrations of unique mammalian diversity worldwide (Heaney et al., 1998). These species are usually not widely distributed within the Philippines but rather are confined to one or a few islands. Recent studies have shown that the geological history of the archipelago is largely responsible for the pattern of distribution, with most species of mammals found on only one of the several islands that formed during periods of low sea level in the late and middle Pleistocene. Each of these Pleistocene islands is surrounded by deep water (greater than 120 m current

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depth), and each has remained as an isolated oceanic island throughout its existence. However, though they are isolated by deep-water channels, the channels are not wide, usually not more than 25 km and often much narrower (Heaney, 1986, 1991, 1993, 2004; Heaney and Rickart, 1990; Heaney & Regalado, 1998).

Camiguin Island was noted by Heaney (1984, 1986) as an apparent exception to this pattern: collections made on Camiguin in the 1960s by field teams from Silliman University did not include any endemic mammals, even though the island seemed large enough to support them (Heaney, 1986, 2004). After the discovery of four endemic species on Sibuyan Island, another small oceanic island in the archipelago (Goodman & Ingle, 1993; Heaney et al., 1998), we suspected that the mammals of Camiguin might not have been fully surveyed, so we returned in 1994 and 1995 for further investigations (Heaney et al., 2004; Heaney & Tabaranza, 2006). In the course of those field studies, we documented the presence of two previously unknown species of mammals (Heaney & Tabaranza, 1997), *Bullimus gamay* (Rickart et al., 2002) and a species of forest mouse, genus *Apomys*. It is the purpose of this paper to describe this new species of forest mouse.

Materials and Methods

Specimens examined for this study are housed in the Delaware Museum of Natural History (DMNH), Field Museum of Natural History (FMNH), Mindanao State University–Iligan Institute of Technology (MSU-IIT), National Museum of the Philippines (NMP), University of Michigan Museum of Zoology (UMMZ), and United States National Museum of Natural History (USNM). Half the specimens from Camiguin now housed in FMNH will be sent to NMP. Material examined included specimens prepared as study skins with skulls (and some with postcranial skeletons), complete skeletons, and formalin-fixed specimens stored in 70% ethyl alcohol, many with skulls subsequently removed and cleaned. The following samples were examined: *Apomys hylocoetes*—Mindanao Island: Bukidnon Province: Mt. Kitanglad Range: 15 km S, 12.5 km W Dalwangan, elev. 2800 m, FMNH 148055; 16.5 km S, 4 km E Camp Phillips, elev. 1900 m, FMNH 147871–872, 148123–124; 18.5 km S, 4 km E camp Phillips, elev. 2250 m, FMNH 147874–876, 147880, 147900–904, 147906, 148125–128, 148132, 148135–138. *Apomys insignis*—Mindanao Island: Bukidnon Province: Mt. Kitanglad Range: 16.5 km S, 4 km E Camp Phillips, elev. 1900 m, FMNH 148152; 17 km S, 7 km E Baungon, elev. 1550 m, FMNH 146703; 18 km S, 7 km E Baungon, elev. 1800 m, FMNH 146704–710, 146712–714, 146716–718, 147088–089, 147091–092, 147094, 147098–099, 147102. *Apomys* sp.—Biliran Island: 3½ km S, 5½ km W Caibiran, elev. 700 m, UMMZ 160314, 160290, 160429–430; 4½ km S, 5 km W Caibiran, elev., 920 m, UMMZ 160290–291, 160315–316. Leyte Island: 9 km N, 3 km E Baybay, elev. 750 m, UMMZ 160318; 8½ km N, 2½ km E Baybay, elev. 500 m, UMMZ 160317, 160441. *Apomys* n. sp.—Holotype and referred specimens from Camiguin Island (see below).

Specimens were assigned to age categories as follows. Subadult animals are those that have not completed cranial growth, especially those having unfused basicranial sutures; these young animals have pelage that is usually softer and grayer than that of adults and are noticeably lower in weight, and females are usually nulliparous. Young adults are older; they have unworn adult pelage and have nearly completed cranial growth but have not yet reached adult weight and usually have not yet reproduced or are pregnant for the first time. Adults have completed cranial growth and have adult pelage, and usually the females are multiparous. Terminology for description of external features follows Brown (1971) and Brown and Yalden (1973). Terminology for cranial and dental features follows Musser and Heaney (1992). Scanning electron micrographs of skulls and teeth were made with uncoated specimens.

External measurements (total length, tail length, hind foot length, length of ear from notch, weight in grams) were taken from collectors' field catalogs or specimen labels. Fourteen cranial measurements (Table 1) were taken with digital calipers to the nearest 0.01 mm by Heaney; comparisons made in the text refer only to specimens also measured by Heaney.

Results

The endemic Philippine genus *Apomys* was described by Mearns (1905) to contain three species: *A. hylocoetes* (as the type species), *A.*

TABLE 1. Cranial and external measurements of *Apomys camiguinensis*, *A. hylocoetes*, *A. insignis*, and *A.* sp. (from Leyte and Biliran), in mm. Measurements, defined in the text, are given as mean ± 1 standard deviation, with ranges beneath, for adult males and females (with sample sizes indicated for each species and sex)

	A. camiguinensis		***A. hylocoetes***		***A. insignis***		***A.* sp. (Biliran + Leyte)**	
Measurement	**Males (6)**	**Females (4)**	**Males (12)**	**Females (14)**	**Males (12)**	**Females (13)**	**Males (5)**	**Females (4)**
Basioccipital L	29.09 ± 0.49 28.59–29.24	28.27 ± 0.45(3) 27.84–28.74	28.79 ± 0.46 27.91–29.60	28.44 ± 0.65 27.14–29.58	27.97 ± 0.38 27.20–28.46	27.75 ± 0.63 26.80–28.55	25.28 ± 0.40 24.79–25.61	26.34 ± 0.44 25.93–29.93
Interorbital L	5.25 ± 0.14 5.08–5.39	5.24 ± 0.25 4.92–5.51	5.25 ± 0.20 4.97–5.56	5.18 ± 0.16 4.84–5.51	4.97 ± 0.18 4.60–5.28	4.97 ± 0.15 4.76–5.24	4.83 ± 0.11 4.69–4.99	4.88 ± 0.15 4.68–5.01
Zygomatic B	14.88 ± 0.31 14.41–15.20	14.95 ± 0.39 14.41–15.32	15.2 ± 0.25 14.91–15.77	15.02 ± 0.30 14.60–15.53	14.82 ± 0.37 13.97–15.47	14.74 ± 0.41 13.97–15.35	13.12 ± 0.43 12.61–13.47	13.75 ± 0.25 13.44–13.99
Mastoid B	12.84 ± 0.07(5) 12.75–12.93	12.43 ± 0.42(3) 11.95–12.74	13.07 ± 0.19 12.70–13.42	12.83 ± 0.30 12.46–13.29	12.45 ± 0.34 12.07–13.05	12.35 ± 0.24 12.03–12.95	11.85 ± 0.08 11.76–11.98	11.79 ± 0.32 11.47–12.11
Nasal L	11.36 ± 0.33 10.92–11.80	11.06 ± 0.49 10.48–11.67	12.54 ± 0.30 12.09–13.05	12.40 ± 0.50 11.33–13.19	11.64 ± 0.49 10.93–12.30	11.84 ± 0.53 11.47–13.13	10.33 ± 0.31(4) 9.88–10.59	10.68 ± 0.42 10.22–11.05
Ant. nasal B	3.80 ± 0.24 3.48–4.18	3.68 ± 0.14 3.51–3.84	3.84 ± 0.22 3.50–4.32	3.80 ± 0.24 3.22–4.05	3.79 ± 0.22 3.29–4.12	3.74 ± 0.21 3.48–4.11	3.32 ± 0.16(4) 3.23–3.55	3.59 ± 0.22 3.34–3.87
Rostral D	6.42 ± 0.17 6.18–6.69	6.26 ± 0.09 6.18–6.38	6.30 ± 0.15 6.04–6.46	6.25 ± 0.23 5.82–6.62	6.30 ± 0.17 5.97–6.56	6.32 ± 0.21 5.84–6.65	5.87 ± 0.19 5.62–6.03	6.13 ± 0.35 5.87–6.64
Rostral L	12.00 ± 0.31 11.57–12.48	11.61 ± 0.49 10.89–11.99	13.20 ± 0.42 12.43–13.78	13.10 ± 0.47 12.04–13.75	12.04 ± 0.35 11.54–12.73	12.05 ± 0.55 11.41–13.22	10.63 ± 0.26(4) 10.30–10.92	11.16 ± 0.19 10.87–11.27
Orbital L	10.22 ± 0.20 10.03–10.58	10.26 ± 0.31 9.95–10.67	9.99 ± 0.15 9.76–10.26	9.72 ± 0.23 9.35–10.20	9.96 ± 0.33 9.36–10.39	10.17 ± 0.22 9.78–10.56	9.24 ± 0.16 8.99–9.43	9.57 ± 0.28 9.16–9.76
Maxil. toothrow L	6.00 ± 0.10 5.82–6.37	6.04 ± 0.20 5.90–6.11	6.06 ± 0.32 5.61–6.33	6.04 ± 0.14 5.54–6.85	5.95 ± 0.22 5.87–6.34	5.29 ± 0.08 5.59–6.33	5.20 ± 0.17 5.17–5.37	6.04 ± 0.20 5.01–5.42
Palatal B at M1	6.45 ± 0.18 6.19–6.67	6.35 ± 0.11 6.27–6.51	6.52 ± 0.11 6.33–6.70	6.53 ± 0.18 6.42–6.85	6.64 ± 0.26 6.19–7.02	6.52 ± 0.26 6.16–6.94	5.77 ± 0.20 5.56–6.03	5.74 ± 0.18 5.57–5.99
Diastema L	7.32 ± 0.21 6.91–7.54	7.33 ± 0.16 7.20–7.56	7.35 ± 0.23 7.03–7.65	7.30 ± 0.39 6.70–7.99	7.04 ± 0.29 6.69–7.58	6.98 ± 0.29 6.59–7.42	6.47 ± 0.18 6.27–6.66	6.84 ± 0.22 6.70–7.17
Total L	260.2 ± 4.4 254–266	253.8 ± 6.6 246–262	251.9 ± 6.3 240–260	247.8 ± 7.2 239–260	251.9 ± 10.3 231–266	251.8 ± 10.5 236–272	237.8 ± 6.3 231–247	245 ± 14.50(3) 230–259
Tail L	147.8 ± 7.4 140–160	146.3 ± 4.8 140–150	142.0 ± 5.2 133–150	140.5 ± 7.7 127–149	147.0 ± 4.4 139–154	146.4 ± 9.3 134–162	140.2 ± 5.1 135–146	145.0 ± 14.7(3) 132–161
Hind foot L	33.2 ± 0.4 (5) 33–34	32.5 ± 1.3 31–34	31.7 ± 1.20 29–33	31.6 ± 1.0 30–34	33.4 ± 0.8 32–35	32.8 ± 1.08 31–35	31.0 ± 0.70 30–32	30.0 ± 0.70(3) 29–32
Ear L	19.0 ± 0.00 (5) 19.0	19.0 ± 1.00(3) 18–20	20.3 18–22	20.1 ± 0.5 19–21	1.00 18–21	20.1 ± 0.5 18–20	19.8 ± 1.00(11) 18–19	19.3 ± 0.65 19–20
Weight (g)	41.1 ± 5.4 33–48.5	38.5 ± 3.5 34–42	39.5 ± 3.0 34–45	36.6 ± 2.6 33–40	37.8 ± 2.3 35–41	38.0 ± 5.7 33–52	27.8 ± 2.8 24–31	31.5 ± 3.7(3) 27–32

insignis, and *A. petraeus* (the last synonymized with *A. hylocoetes* by Musser, 1982), all from Mt. Apo, from which the name was derived. As related by Musser (1982), additional species were named from Luzon and Catanduanes, and the genus was found throughout much of the archipelago (Ruedas, 1995; Heaney et al., 1998). However, because the initial description was vague and many genera of Indo-Australian rodents poorly studied, *Apomys* was briefly synonymized with the genus *Rattus* at a time when most Indo-Australian murids were placed in that genus. Musser (1982) thoroughly redescribed *Apomys*, pointing out its many distinctive characters, and redefined the species then known. Musser and Heaney (1992) further defined and compared *Apomys* to other Philippine murids, and they pointed out its apparent close relationship to *Chrotomys, Celaenomys*, and *Rhynchomys*, also endemic to the Philippines. Using data from Musser and Heaney (1992), Heaney and Rickart (1990) postulated that *Apomys* was basal to the clade including *Chrotomys, Celaenomys*, and *Rhynchomys* and noted the diversification of this clade within the Philippines as an example of adaptive radiation. Heaney et al. (1998) noted the presence of many undescribed species of *Apomys*, including the species from Camiguin reported by Heaney and Tabaranza (1997).

Rickart and Heaney (2002) showed that *Apomys hylocoetes, A. insignis*, and the Leyte *Apomys* (as well as most others from Greater Luzon and Greater Negros-Panay) have distinctive karyotypes, but the *Apomys* from Camiguin has not been karyotyped. Steppan et al. (2003) used molecular data to assess phylogenetic relationships and geographic patterns of diversification within *Apomys*. Analysis of variation in cytochrome-b in 10 species (Fig. 1) showed the presence of three major clades: one containing *Apomys datae* and *A. gracilirostris*; a second clade containing *A. microdon, A. musculus*, and two undescribed species from Negros and Sibuyan (the "Greater Luzon, Mindoro, and Negros clade"); and a third clade containing *A. hylocoetes* and *A. insignis* from Mindanao, plus an undescribed species from Leyte, Biliran, and Bohol and another from Camiguin (the "Greater Mindanao clade"). The second and third of these three clades form a monophyletic clade that Musser (1982) described as being "species . . . of small or medium body size in which the canal for the internal maxillary artery [also described as the infraorbital branch of the stapedial artery] is partially open and part of the artery is exposed on the ventral surface of each pterygoid plate. That feature, combined with bright tawny upperparts, buffy underparts, brown or pale buffy feet, and patterning on the tail (usually monocolored or mottled, rarely sharply bicolored) suggest the five species [known in 1982] may be more closely related to each other than to any others in *Apomys*." Musser's (1982) recognition and diagnosis of this clade, based on very few specimens, was prescient and remains accurate. In the analysis by Steppan et al. (2003), the species from Camiguin is basal to the others in the "Greater Mindanao clade" (Fig. 1), and they estimated the time of divergence of the Camiguin mouse from the other members of its clade at about 2.3 million years ± about 25%.

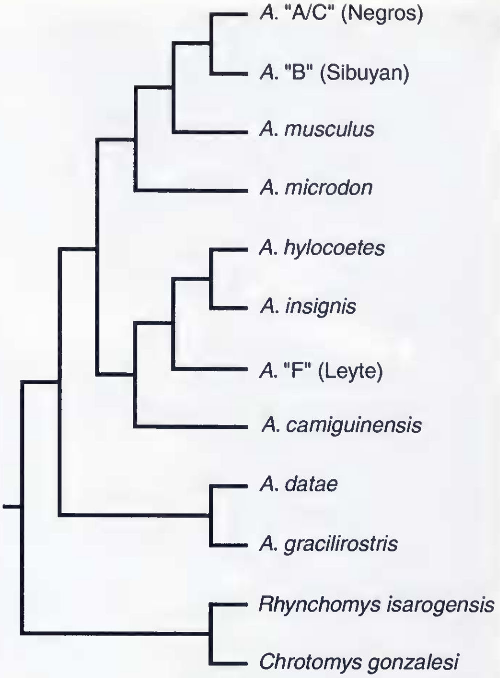

FIG. 1. Hypothesis of phylogenetic relationships within the genus *Apomys* based on parsimony analysis of cytochrome-b molecular data (based on Steppan et al., 2003).

We note that the *Apomys* from Biliran, Bohol, and Leyte (which we hereafter refer to as "the Leyte *Apomys*") was tentatively considered to represent either *A. microdon* (by Musser, 1982) or *A. littoralis* (Rickart et al., 1993; Heaney et al.,

FIG. 2. Photograph of an adult *Apomys camiguinensis*, taken on Mt. Timpoong, Camiguin Island, in March 1995.

1998), but the combination of the morphological data presented here, karyotypic data (Rickart & Heaney, 2002), and molecular data (Steppan et al., 2003) have led us to conclude that the Leyte *Apomys* is a distinct species; further details and description will be published elsewhere.

The specimens from Camiguin are morphologically similar to series of *A. hylocoetes* and *A. insignis* from Mindanao and the undescribed species from Leyte and Biliran but readily distinguished from all three of these species on the basis of external and cranial features. Heaney et al. (1998) and Steppan et al. (2003) referred to this animal informally as "*Apomys* sp. D." We now name the species from Camiguin as *Apomys camiguinensis*, new species.

Apomys camiguinensis, new species

Holotype—Adult male, FMNH 167878, collected 16 May 1994 by B. R. Tabaranza, Jr. Specimen originally fixed in formalin, transferred to 70% ethyl alcohol with skull removed and cleaned. Specimen is currently on deposit at FMNH and is to be transferred to NMP.

Type Locality—Barangay Kital-is, Sagay Municipality, 2 km N, 62 km W Mahinog, 1000 m elevation, Camiguin Province, Camiguin Island. 9°9.5′N, 124°43.5′E (see Heaney & Tabaranza, 2006, for further details).

Referred Specimens and Localities—In addition to the holotype, 19 paratypes are known from three localities ranging from 1000 to 1400 m (FMNH 154815–154816, 154854–154860, 167878–167882, plus 6 specimens at MSU-IIT); for localities, see Heaney et al. (2006). All were originally preserved in formalin and are now stored in ethyl alcohol, many with skulls removed and cleaned, or were prepared as complete skeletons. Tissue samples are housed at FMNH. Half of the specimens will be deposited at NMP.

Distribution—Known only from the upper elevations on Mt. Timpoong, Camiguin Island, but probably occurring throughout the montane and mossy rain forest on Camiguin Island (see fig. 2 in Heaney et al., 2004) and possibly at lower elevations.

Measurements—Table 1.

Etymology—The specific name refers to the sole island on which the species is found. We suggest the common English name "Camiguin forest mouse."

Diagnosis—A species of the genus *Apomys*, as defined by Musser (1982) and Musser and Heaney (1992), including the following distinctive generic features: rostrum long and moderately narrow; viewed laterally, rostrum with a rectangular shape, with premaxillaries projecting well anterior to the anterior edge of the upper incisors; incisive foramina broad relative to length; bony palate wide and long, densely pitted and perforated; upper third molar reduced to a large round peg; lower third molar also peg-like but retaining an anterior lamina, without evidence of the two cusps that usually form this lamina; occlusal surface of each first and second upper molar consisting of two simple chevron-shaped laminae followed by a small oval lamina, without evidence of cuspidation; auditory bulla separated from the squamosal and alisphenoid by a gap that is formed by the coalescence of the postglenoid foramen, the postalar fissure, and the middle lacerate foramen.

As described in more detail in the following section, the Camiguin mouse is defined by the following characters or unique combination of characters: moderate body size but somewhat robust build for the genus overall; the tail is long relative to body length, with unusually large scales, and more often with a sharp transition from dark brown dorsum to pale brown venter (i.e., sharply bicolored) than in other species; moderately long but unusually broad hind foot with small plantar pads, and slightly shorter ear. The pelage has more brown in the generally russet-brown dorsum than on its closest relatives and has more conspicuous salt-and-pepper speckling dorsally; the mystacial and genal vibrissae are long but moderate for the genus. The cranium has an unusually long braincase and orbit, somewhat narrow zygomatic and mastoid width, and a moderately long but deep and robust rostrum. The palate is rather narrow, the posterior edge of the palate extends unusually far posterior to the last molar, the incisive foramina long and wide, and the distance from the posterior edge of the incisive foramina is unusually short. The longest axis of the bullae is about 35° from the midline axis of the skull. The toothrows are of moderate size; the anterolabial cusp of the third upper molar is barely evident in most individuals.

Description and Comparisons—*Apomys camiguinensis* is an attractive mouse with large eyes and ears, long tail, and soft pelage (see Frontispiece, this volume, and Fig. 2). As with other members of the genus, the pelage is soft and dense, without spines or stiff hairs. The dorsal coloration is a rich brownish-russet with a small amount of salt-and-pepper speckling; underfur is pale slate-gray. The venter is paler, usually nearly white with a wash of buffy or pale russet, but some individuals have blazes of pure white (usually on the chest) or are much darker brown or russet-brown. There is a narrow area of bare skin around the eyes; the ears are moderately dark brown, with short hairs apparent on the outer surface, and present but tiny and nearly invisible on the inner surface. The mystacial vibrissae are long and conspicuous. The dorsal surface of the fore and hind feet are mostly buffy or pale brown but with a narrow band of scattered darker hairs around the midline, and these decrease in number and length toward the distal end of each foot (with only pale hairs on the dorsal surface of the toes). The feet are lightly pigmented or unpigmented on the ventral surface, with conspicuous plantar pads on the ventral surface (Fig. 3). The tail is long with conspicuous scales; fine hairs that are present between the scales are most visible on the dorsal and lateral surfaces and least visible ventrally. The tail is darker on the dorsal surface than on the ventral surface. The scrotum of adult males is fairly small and projects beyond the abdomen only partially on the posterior portion and has black or dark brown pigment at the posterior tip, about 3–5 mm in length. Females have two pairs of inguinal mammae.

Apomys camiguinensis is easily distinguished from most members of the genus by its intermediate size (only *A. insignis* and *A. hylocoetes* are similar) and from those two species by both external and cranial characters. *Apomys camiguinensis* has total length (average 254–260 mm) slightly greater than *A. hylocoetes* (248–252 mm) and *A. insignis* (251–252 mm) and substantially greater than the Leyte *Apomys* (238–245 mm; Table 1). The average tail length (146–148) is equal to that of *A. insignis* (147–148 mm), and substantially longer than that of *A. hylocoetes* (141–142 mm) and the Leyte *Apomys* (140–145 mm). The tail averages 57% of the total length in *A. camiguinensis*, compared

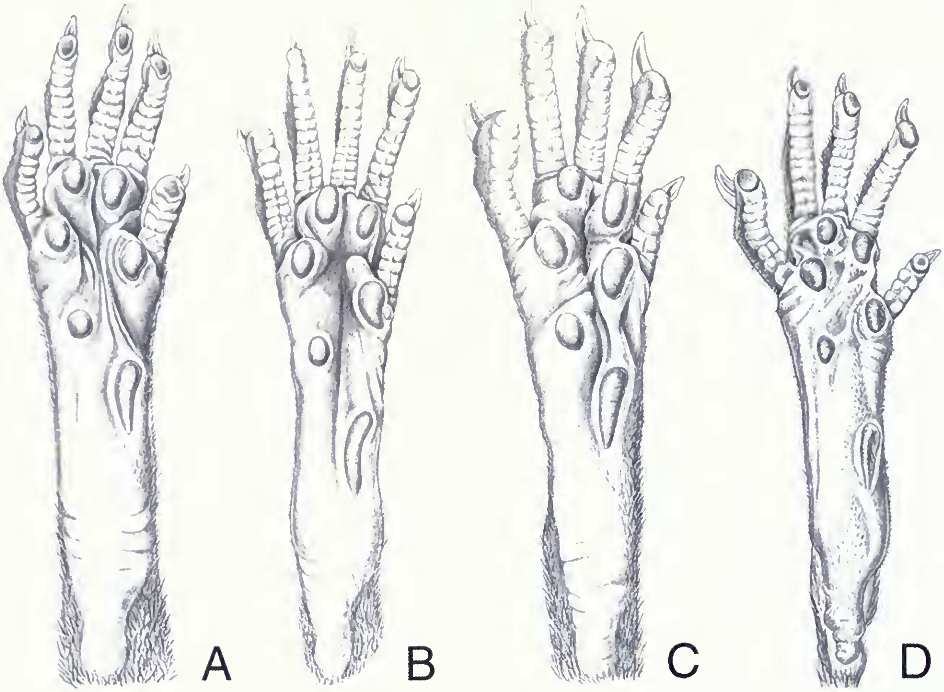

FIG. 3. Ventral surface of the right hind feet of (**A**) *Apomys camiguinensis*, (**B**) *A. hylocoetes*, (**C**) *A. insignis*, and (**D**) the undescribed *Apomys* from Leyte, all to roughly the same scale. Those of *A. hylocoetes* and *A. insignis* are redrawn from Musser (1982).

to 56.5% in *A. hylocoetes*, 58% in *A. insignis*, and 59% in the Leyte *Apomys*. The hind foot (about 33 mm) is about equal in length to that of *A. insignis* (33 mm) and is substantially longer than in *A. hylocoetes* (31–32 mm) and the Leyte *Apomys* (30–31 mm); the hind foot of *A. hylocoetes* is notably the broadest (Fig. 3; see also fig. 7 in Musser, 1982). Ear length is greatest in *A. hylocoetes* (20.2 mm), with *A. insignis* (19.5 mm), *A. camiguinensis* (19.0 mm), and the Leyte *Apomys* (18–19 mm) progressively slightly smaller (Table 1). The weight of *A. camiguinensis* (38–41 g) averages the greatest of the four, followed by *A. hylocoetes* (36–39 g), *A. insignis* (37–38 g), and the Leyte *Apomys* (28–31 g). In other words, the Camiguin *Apomys* is relatively heavy and long and has a relatively long tail (but slightly less long proportionately than some close relatives), a moderately long hind foot, and somewhat short ear.

The following qualitative external characters also distinguish *Apomys camiguineusis* from its three closest relatives. The dorsal coloration of the Camiguin mouse is less russet and more brown than in *A. hylocoetes* and *A. insignis*, with more of the salt-and-pepper appearance; the Leyte mouse is dorsally brighter red than the others, with more red and orange in the russet than the other three and almost no salt-and-pepper. Ventral coloration is generally similar in all four, though with the variation noted above, but *A. hylocoetes* tends to have more of an orange wash than the others. The dorsal surface of the hind feet usually is palest in the Leyte mouse and darkest in the Camiguin mouse. The mystacial vibrissae are long on all four species but longest on *A. insignis* (up to 56–60 mm maximum), on which they reach past the middle of the back, and intermediate on the Camiguin mouse (52–55 mm), *A. hylocoetes* (51–55 mm), and Leyte mouse (50–55 mm). Genal vibrissae reach to the anterior edge of the largest lateral pad on the Camiguin and Leyte mice but farther forward, to the base of the toes, on *A. hylocoetes* and *A. insignis*.

The hind foot (Fig. 3) differs markedly among the four. The foot of *A. camiguinensis* is about the same length as that of *A. hylocoetes* but is broader and has smaller plantar pads. The hind foot of the Leyte mouse is proportioned similarly

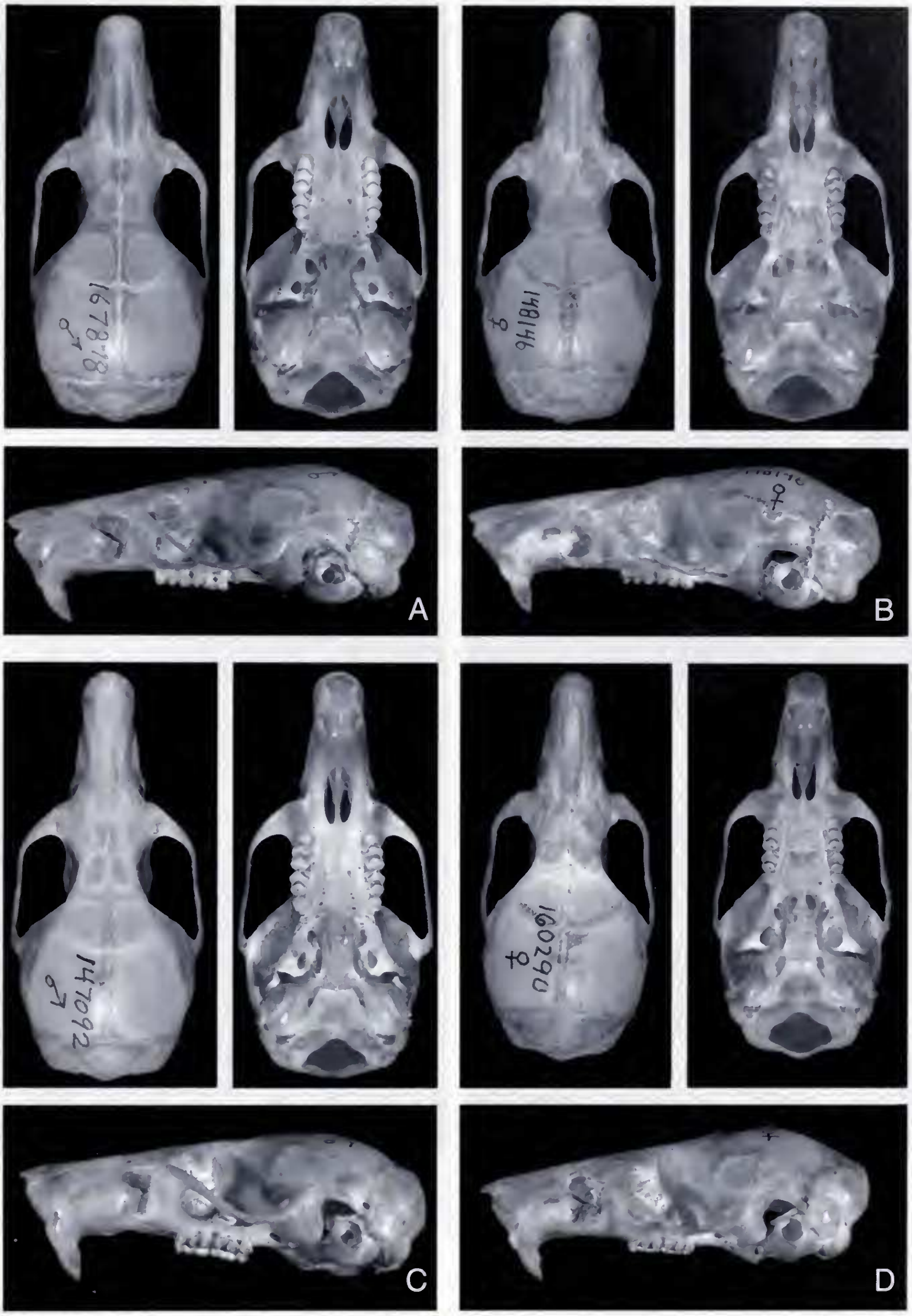

FIG. 4. Photographs of dorsal, ventral, and lateral views of the crania of *Apomys camiguinensis* (**A**; FMNH 167878, holotype), *A. hylocoetes* (**B**; FMNH 148146), *A. insignis* (**C**; FMNH 147092), and the undescribed *Apomys* from Leyte (**D**; UMMZ 160290), all to the same scale.

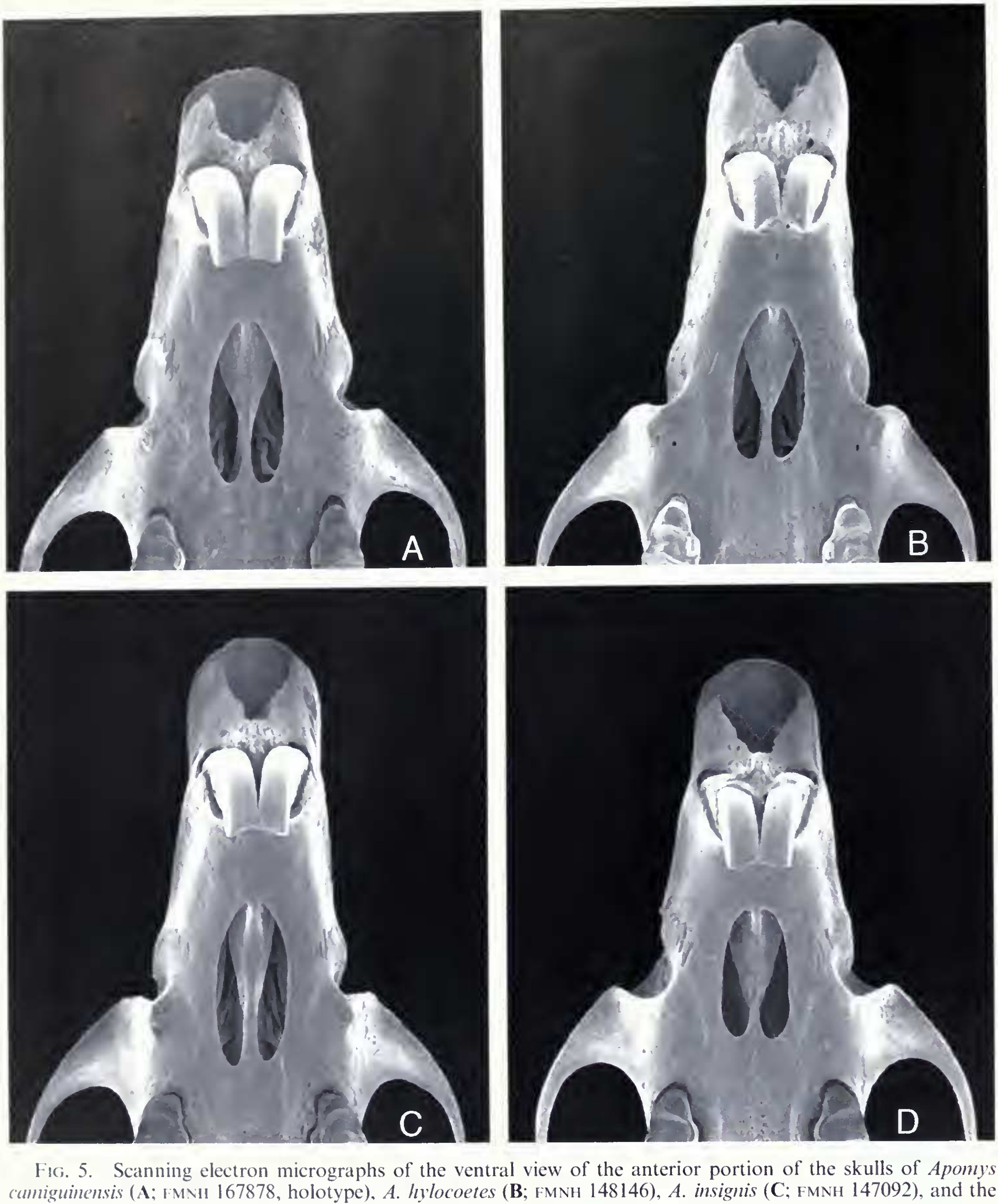

Fig. 5. Scanning electron micrographs of the ventral view of the anterior portion of the skulls of *Apomys camiguinensis* (**A**; FMNH 167878, holotype), *A. hylocoetes* (**B**; FMNH 148146), *A. insignis* (**C**; FMNH 147092), and the undescribed *Apomys* from Leyte (**D**; UMMZ 160290), all to same scale.

to *A. hylocoetes* but is smaller. The hind foot of *A. insignis* is very long and narrow, with plantar pads of moderate size. On all species, the claws on all five digits are unpigmented and laterally compressed. On *A. camiguinensis*, the claws are sturdy and sharply pointed; those of *A. hylocoetes* are slightly thinner and more sharply pointed and the digits bearing them slightly more slender. The digits and claws of *A. insignis* are shorter and more slender; the digits and claws of

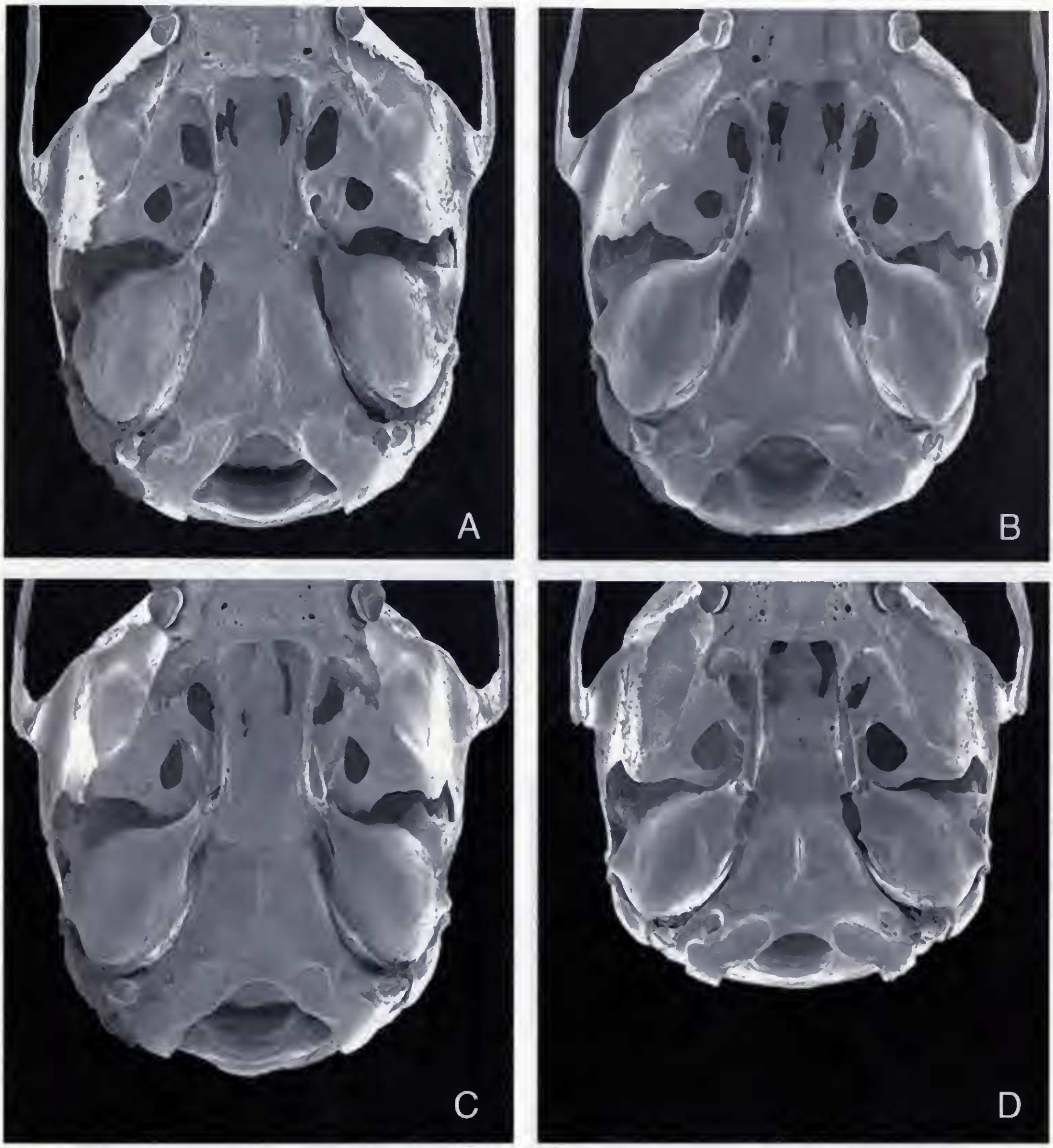

FIG. 6. Scanning electron micrographs of the ventral view of the posterior portion of the skulls of *Apomys camiguinensis* (**A**; FMNH 167878, holotype), *A. hylocoetes* (**B**; FMNH 148146), *A. insignis* (**C**; FMNH 147092), and the undescribed *Apomys* from Leyte (**D**; UMMZ 160290), all to same scale.

the Leyte mouse are still smaller and more slender. The forefeet of *A. camiguinensis* have smaller pads than those of the others (but only proportionately in the case of the generally smaller Leyte mouse), but the feet are slightly broader and more robust than in the other species. All four species have a flat, unpigmented nail on the pollex. The relative size and thickness follows the same pattern as the hind feet, with *A. camiguinensis* being the most robust, *A. hylocoetes* slightly shorter and thinner, *A. insignis* much shorter and more slender, and the Leyte mouse much like *A. insignis* but a bit smaller overall.

The tail scales on the Camiguin mouse are largest, with 12–12.5 scales/cm near the base, compared to 14–15 scales/cm in *A. hylocoetes*, 13–14 in *A. insignis*, and 13–15 in the Leyte

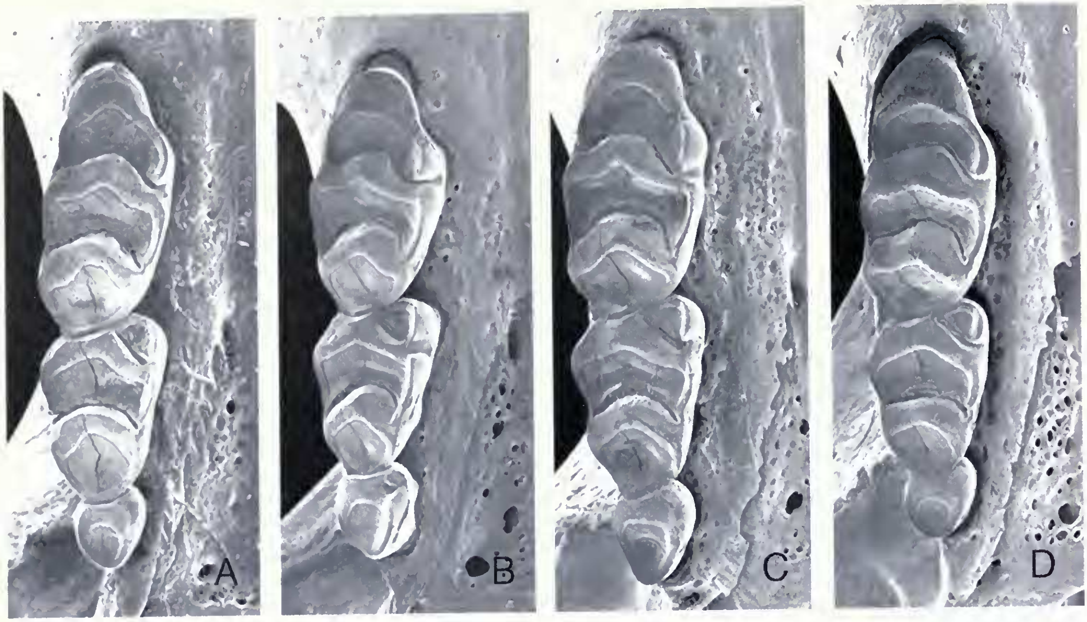

FIG. 7. Scanning electron micrographs of the occlusal surface of the maxillary toothrows of *Apomys camiguinensis* (**A**; FMNH 167878, holotype), *A. hylocoetes* (**B**; FMNH 148146), *A. insignis* (**C**; FMNH 147092), and the undescribed *Apomys* from Leyte (**D**; UMMZ 160290), all to same scale.

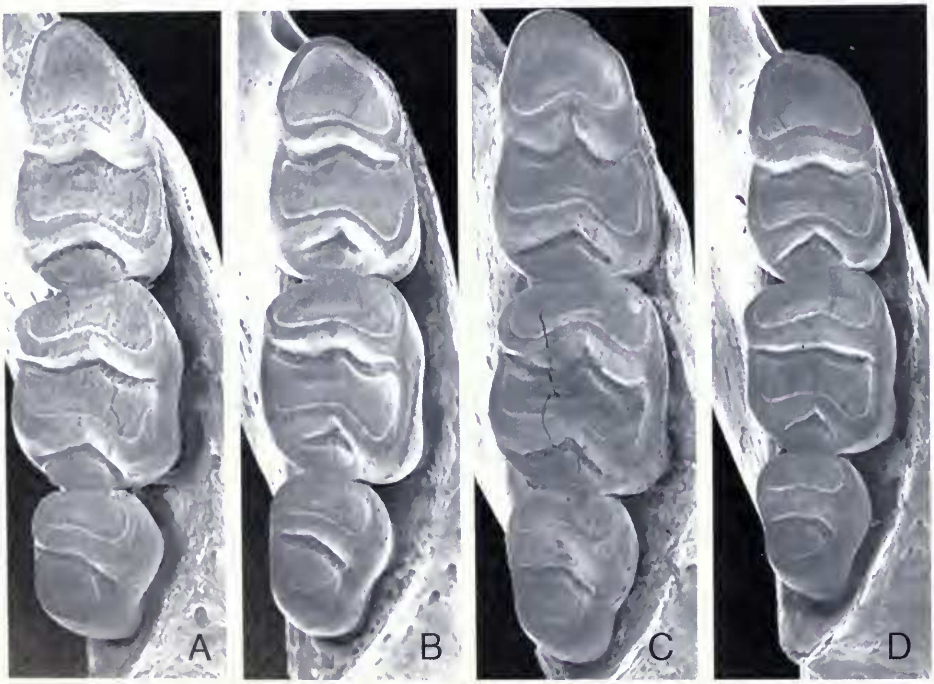

FIG. 8. Scanning electron micrographs of the occlusal surface of the mandibular molariform toothrows of *Apomys camiguinensis* (**A**; FMNH 167878, holotype), *A. hylocoetes* (**B**; FMNH 148146), *A. insignis* (**C**; FMNH 147092), and the undescribed *Apomys* from Leyte (**D**; UMMZ 160290), all to same scale.

mouse. The size of the scales remains about the same more distally on a given species to about the midpoint; from there to the tip scale size decreases, mostly in the last quarter of the length, to about half the length (and one-fourth the size) of scales near the base of the tail. The scales of the tail are dark brown dorsally and nearly white ventrally on all four species, but the transition is most often an abrupt line on the Camiguin mouse, often producing a sharply bicolored tail, and most often gradual on the other three species. Typically, three hairs grow from beneath each scale, projecting only slightly laterally from the tail; on the basal quarter of the tail, one of the three hairs is missing from a given scale about one-third of the time. On *A. camiguinensis*, the hairs are about one and one-third the length of a scale near the base of the tail, have about the same length 25% toward the tip, are slightly longer at the midpoint, are about one and two-thirds the length of a scale 75% toward the tip, and are about five times the length of a scale near the tip, where scale length has been reduced by about half relative to the base. On *A. hylocoetes*, hairs are about one and a half the length of a scale near the base of the tail, are similar 25% toward the tip, are about twice the length of a scale near the midpoint, are about two and a half times the length of a scale 75% toward the tip, and are more than five times the length of a scale near the tip. On *A. insignis*, hairs are one and one-third a scale length near the tail's base, similar at 25%, one and two-thirds near the midpoint, about two and one-half of a scale length near 75%, and about three and one-half the length of a scale near the tip. On the Leyte mouse, tail hairs are slightly less than the length of a scale near the base of the tail, similar at the midpoint and at 75%, and about two times the length of a scale near the tip. In all four species, the hair becomes slightly greater in diameter distally than it is proximally; combined with the trend for greater length, this means that the tail become more heavily covered with hair distally. None of the species shows elongated hairs at the very tip of the tail (i.e., there is no "pencilling"). Hairs on the dorsal surface are more heavily pigmented dorsally than ventrally in all four species. On adults of all four species, the dorsal surface of the tip (2–5 mm) of the tail becomes worn, with most scales and many hairs absent, leaving a smooth, leathery surface.

The cranium of *Apomys camiguinensis* (Figs. 4–6) has basioccipital length (28.3–29.0 mm) slightly greater than that of *A. hylocoetes* (28.3–28.8 mm), clearly more than *A. insignis* (27.8–28.0 mm) and substantially more than the Leyte *Apomys* (25.3–26.3 mm); the interorbital width is proportioned similarly (Table 1). Zygomatic breadth averages greatest in *A. hylocoetes* (15.0–15.2 mm), followed by *A. camiguinensis* (14.9–15.0 mm), *A. insignis* (14.7–14.8 mm), and the Leyte *Apomys* (13.1–13.7 mm), with mastoid breadth following the same pattern (Table 1). Nasal length averages substantially greater in *A. hylocoetes* (12.3–12.5 mm) than in *A. insignis* (11.6–11.9 mm), *A. camiguinensis* (11.1–11.4 mm), or the Leyte *Apomys* (10.3–10.7 mm), and anterior nasal breadth is similarly patterned (Table 1). Rostral depth averages greatest in *A. camiguinensis* (6.3–6.4 mm), with *A. hylocoetes* (6.2–6.3 mm) and *A. insignis* (6.3 mm) slightly less deep and very similar to each other and the Leyte *Apomys* generally less deep (5.9–6.1 mm). Rostral length (Fig. 5) is clearly greatest in *A. hylocoetes* (13.1–13.2 mm), with *A. camiguinensis* (11.6–12.0 mm) and *A. insignis* (11.9–12.0 mm) similar to each other but much greater than the Leyte *Apomys* (10.6–11.2 mm). Orbital length averages greatest in *A. camiguinensis* (10.2–10.3 mm), followed by *A. insignis* (10.0–10.2 mm) and *A. hylocoetes* (9.7–10.0) and the small Leyte *Apomys* (9.2–9.6). To summarize, *A. camiguinensis* is characterized by the longest skull and deepest rostrum, but *A. hylocoetes* has slightly greater zygomatic and mastoid width as well as greater nasal length and breadth and rostral length. Although the rostrum of *A. camiguinensis* is moderate in length, the orbital region and braincase are unusually long. The cranium of *A. insignis* tends to be smaller but generally similarly proportioned to *A. camiguinensis*, and the Leyte *Apomys* is smaller in all dimensions, though it seems to follow the pattern of *A. camiguinensis* and *A. insignis*.

The maxillary toothrow (Fig. 7) of *A. camiguinensis* (6.0 mm) averages nearly identical in length to that of *A. hylocoetes* (6.0 mm) and *A. insignis* (6.0 mm), and all are much greater than that of the Leyte *Apomys* (5.2–5.3 mm). Palatal breadth at M^1 (Fig. 4) is greatest in *A. insignis* (6.5–6.6 mm), followed by *A. hylocoetes* (6.5 mm) and *A. camiguinensis* (6.3–6.5 mm) and the Leyte *Apomys* (5.7–5.8 mm). Diastema length (Figs. 4 and 5) in *A. camiguinensis* (7.3 mm) averages slightly greater than in *A.*

hylocoetes (7.2–7.3 mm), more than *A. insignis* (7.0 mm), and least in the Leyte *Apomys* (6.5–6.8 mm). In other words, the maxillary toothrows of the three larger *Apomys* are all similar, with the Leyte *Apomys* having disproportionately short toothrow, but the palate of *A. camiguinensis* is disproportionately narrow (as is that of the Leyte *Apomys*), and that of *A. hylocoetes* is disproportionately wide.

In addition, we note the following qualitative characters. The incisive foramina (Fig. 5) are widest in *A. camiguinensis* and in *A. hylocoetes* and longest in *A. camiguinensis* and *A. insignis*, so that the area of the foramina is greatest in *A. camiguinensis*. The distance from the posterior edge of the incisive foramina to a line between the anterior edges of the first maxillary molar is shortest in *A. camiguinensis*, slightly greater in *A. insignis*, and longest in *A. hylocoetes* and the *Apomys* from Leyte. The braincase of *A. camiguinensis* is slightly more elongate and that of the Leyte *Apomys* proportionately most squarish among the four species (Fig. 6). The posterior edge of the bony palate (Fig. 6) extends farthest posterior to the posterior edge of the last maxillary molar in *A. camiguinensis*, slightly less far in *A. hylocoetes* and the *Apomys* from Leyte, and least far in *A. insignis*. The long axis of the bullae (Fig. 6) is about 45° from the cranial midline axis in the *Apomys* from Leyte, about 40° in *A. hylocoetes* and *A. insignis*, and about 35° in *A. camiguinensis*. The hard palate of *A. hylocoetes* and the Leyte *Apomys* are usually most heavily pitted and perforated with vacuities and *A. camiguinensis* and *A. insignis* less so (Figs. 4 and 7). The third upper molar (Fig. 7) has an anterolabial cusp (probably t1; see Musser & Heaney, 1992, p. 65) that is well developed in *A. hylocoetes*, less conspicuous in *A. insignis*, and barely evident in *A. camiguinensis* and the *Apomys* from Leyte. The first upper molar of *A. hylocoetes* tends to have a more conspicuous anterolingual cleft than do the other three species (Fig. 7). Both upper and lower toothrows of *A. insignis* are the most massive (Figs. 7 and 8), with *A. camiguinensis* somewhat less massive, *A. hylocoetes* substantially less so, and the *Apomys* from Leyte smallest overall. All four species have the canal for the infraorbital branch of the stapedial artery partially open and part of the artery exposed on the ventral surface of each pterygoid plate (Fig. 6), as noted by Musser (1982).

Ecology—See Heaney et al. (2006) for ecological information.

Discussion

The presence of *Apomys camiguinensis* as an endemic species on a small island, along with the additional murine rodent *Bullimus gamay* (Rickart et al., 2002) and the Hanging-Parrot (*Loriculus* sp., described in this volume), as noted above, clearly indicates the importance of Camiguin Island as a unique center of biological diversity that is worthy and in need of conservation (Heaney & Tabaranza, 2005). In addition, the distinctiveness of this species confirms predictions made on the basis of biogeographic models (Heaney, 2004) of the expected presence of endemic small mammals on Camiguin. Further studies of the mammals, birds, and other organisms are clearly warranted to determine, for example, the degree of genetic difference from closest relatives (most of which occur on Mindanao) as a means of assessing the role of colonization and gene flow in determining patterns of species richness and endemism in the Philippines. In other words, Camiguin represents a natural experiment, as a young oceanic, volcanic island that is near to a large, rich source of species (Mindanao), in which we can measure the impact of genetic isolation in animals and plants of varying vagility under standardized conditions. Such studies are certain to produce new insights into the process by which biological diversity is generated in the Philippines and in other oceanic archipelagos.

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Literature Cited

BROWN, J. C. 1971. The description of mammals, 1. The external characters of the head. Mammal Review, **1:** 151–168.

BROWN, J. C., AND D. W. YALDEN. 1973. The description of mammals, 2. Limbs and locomotion of terrestrial mammals. Mammal Review, **3:** 107–134.

GOODMAN, S. M., AND N. R. INGLE. 1993. Sibuyan Island in the Philippines—Threatened and in need of conservation. Oryx, **27:** 174–180.

HEANEY, L. R. 1984. Mammals from Camiguin Island, Philippines. Proceedings of the Biological Society of Washington, **97:** 119–125.

———. 1986. Biogeography of mammals in Southeast Asia: Estimates of rates of colonization, extinction, and speciation. Biological Journal of the Linnean Society, **28:** 127–165.

———. 1991. An analysis of patterns of distribution and species richness among Philippine fruit bats (Pteropodidae). Bulletin of the American Museum of Natural History, **206:** 145–167.

———. 1993. Biodiversity patterns and the conservation of mammals in the Philippines. Asia Life Sciences, **2:** 261–274.

———. 2004. Conservation biogeography in oceanic archipelagoes, pp. 345–360. *In* Lomolino, M. V. and L. R. Heaney, eds., Frontiers of Biogeography: New Directions in the Geography of Nature. Sinauer Associates, Sunderland.

HEANEY, L. R., D. S. BALETE, L. DOLAR, A. C. ALCALA, A. DANS, P. C. GONZALES, N. R. INGLE, M. LEPITEN, P. S. ONG, W. L. R. OLIVER, E. A. RICKART, B. R. TABARANZA, JR., AND R. C. B. UTZURRUM. 1998. A synopsis of the mammalian fauna of the Philippine Islands. Fieldiana Zoology, n.s., **88:** 1–61.

HEANEY, L. R., AND J. C. REGALADO, JR. 1998. Vanishing Treasures of the Philippine Rain Forest. The Field Museum, Chicago.

HEANEY, L. R., AND E. A. RICKART. 1990. Correlations of clades and clines: Geographic, elevational, and phylogenetic distribution patterns among Philippine mammals, pp. 321–332. *In* Peters, G. and R. Hutterer, eds., Vertebrates in the Tropics. Museum Alexander Koenig, Bonn.

HEANEY, L. R., AND B. R. TABARANZA, JR. 1997. A preliminary report on mammalian diversity and conservation status of Camiguin Island, Philippines. Sylvatrop, **5**(1995): 57–64.

———. 2006. Introduction to the mammal and land bird faunas of Camiguin Island, Philippines, pp. 1–13. *In* Heaney, L. R., ed., The Mammals and Birds of Camiguin Island, Philippines, a Distinctive Center of Biodiversity. Fieldiana Zoology, n.s., **106:** 1–72.

HEANEY, L. R., B. R. TABARANZA, JR., D. S. BALETE, AND N. RIGERTAS. 2006. Synopsis and biogeography of the mammals of Camiguin Island, Philippines, pp. 00–00. *In* Heaney, R. L., ed., The Mammals and Birds of Camiguin Island, Philippines, a Distinctive Center of Biodiversity. Fieldiana Zoology, n.s., **106:** 28–48.

MEARNS, E. A. 1905. Descriptions of new genera and species of mammals from the Philippine Islands. Proceedings of the United States National Museum of Natural History, **28:** 425–460.

MUSSER, G. G. 1982. Results of the Archbold Expeditions, No. 108. The definition of *Apomys*, a native rat of the Philippine Islands. American Museum Novitates, **2746:** 1–43.

MUSSER, G. G., AND L. R. HEANEY. 1992. Philippine rodents: Definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). Bulletin of the American Museum of Natural History, **211:** 1–138.

RICKART, E. A., AND L. R. HEANEY. 2002. Further studies on the chromosomes of Philippine rodents (Muridae: Murinae). Proceedings of the Biological Society of Washington, **115:** 473–487.

RICKART, E. A., L. R. HEANEY, P. D. HEIDEMAN, AND R. C. B. UTZURRUM. 1993. The distribution and ecology of mammals on Leyte, Biliran, and Maripipi Islands, Philippines. Fieldiana Zoology, n.s., **72:** 1–62.

RICKART, E. A., L. R. HEANEY, AND B. R. TABARANZA, JR. 2002. Review of *Bullimus* (Muridae: Murinae) and description of a new species from Camiguin Island, Philippines. Journal of Mammalogy, **83:** 421–436.

RUEDAS, L. A. 1995. Description of a new large-bodied species of *Apomys* Mearns 1905 (Mammalia: Rodentia: Muridae) from Mindoro Island, Philippines. Proceedings of the Biological Society of Washington, **108:** 302–318.

STEPPAN, S., C. ZAWADSKI, AND L. R. HEANEY. 2003. A molecular assessment of phylogenetic relationships and patterns of phylogenesis in the Philippine murid rodent *Apomys*. Biological Journal of the Linnean Society, **80:** 699–715.